Development of internal models and predictive abilities for visual tracking during childhood

Running title: Development of prediction and internal models

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Abstract

Predicting the consequences of our own actions through internal models is an essential component of motor control. Previous studies showed improvement of anticipatory behaviors with age for grasping, drawing and postural control. Since these actions require visual and proprioceptive feedback, these improvements might reflect both the development of internal models and the feedback control. In contrast, visual tracking of a temporarily invisible target gives specific markers of prediction and internal models for eye movements. Therefore, we recorded eye movements in 50 children (aged from 5 to 19 years) and in 10 adults who were asked to pursue a visual target that is temporarily blanked. Results show that the youngest children (5-7y) have a general oculomotor behavior in this task qualitatively similar to the one observed in adults. However, the overall performance of older subjects in terms of accuracy at target reappearance and variability in their behavior was much better than the youngest children. This late maturation of predictive mechanisms with age was reflected into the development of the accuracy of the internal models governing the synergy between the saccadic and pursuit systems with age. Altogether, we hypothesize that the maturation of the interaction between smooth pursuit and saccades that relies on internal models of the eye and target displacement is related to the continuous maturation of the cerebellum.

Introduction

To overcome delays, the control of our actions is based on knowledge about the dynamics of the world and about the future consequences of our actions, which is acquired during development. For instance, anticipatory behaviors are observed in the grip force during object lift (Flanagan and Wing, 1997) or in the forearm in reaction to the unloading of an object (anticipatory postural adjustment – APA, (Hugon et al., 1982)). Such predictive behaviors are acquired early in life (~2 years for grip force (Forssberg et al., 1991) and 3-4 years for APA (Schmitz et al., 1999)), but improve with age and only reach adult-like levels a few years later (8-11 years for grip force (Forssberg et al., 1992) and after 7 years for APA (Girolami et al., 2010)). Prediction of the trajectory of a moving target, which requires an internal model of the environment follows a similar developmental course but only reaches adult levels around 17 years old (van Roon et al. 2008). In addition, the ability of children to learn such predictive behaviors is another key component to better understand the development of internal models. For instance, Vasudevan et al. (2011) showed that young children (< 6 years) could learn the timing but not the spatial coordination during split belt treadmill walking task (with one leg going two times faster than the other). Finally, visual tracking of a visible target moving on a predictable trajectory also evolved with age (Accardo et al., 1995; Haishi and Kokubun, 1995; Salman et al., 2006b), showing that prediction about the dynamics of the world is also acquired during childhood.

All of these actions are driven both by predictive control (based on internal model and state estimation) and by sensory feedback (visual, vestibular, tactile and/or proprioceptive). For instance, smooth pursuit response to a predictably moving target relies both on predictive mechanisms and internal models and on visual feedback

control (Orban de Xivry et al., 2013). Therefore, a pure signature of internal models during development was not obtained by any of the above-mentioned studies.

Such a pure signature of internal models without any interference from sensory feedback can be observed during ocular tracking of temporarily invisible moving targets. Indeed, in the absence of visual feedback, eye movements are only driven by internal models as proprioception does not play any role in the control of eye movements (Wang et al., 2007; Xu et al., 2011). Studies on infants have shown the development in the first months of life of the ability to predict the reappearance of a target that transiently disappeared. At 12 weeks old, infants begin to predict the reappearance (Rosander and von Hofsten, 2004; von Hofsten, 2007). This ability largely increases in the first year of life (Gredebäck and Hofsten, 2004; Bertenthal et al., 2007). However, such predictive mechanisms only refer to the ability to perceive continuous motion and direct their eyes to the other side of the occluder. In contrast, during such blanking periods, adults show more advanced predictive oculomotor responses (Mitrani and Dimitrov, 1978; Becker and Fuchs, 1985; Bennett and Barnes, 2003, 2004, 2005; Madelain and Krauzlis, 2003; Bennett et al., 2007; Coppe et al., 2010). When the target disappears, the smooth pursuit eye velocity typically decreases to a plateau value (Mitrani and Dimitrov, 1978; Becker and Fuchs, 1985). If the duration of blanking is predictable, the eye velocity increases again in anticipation of target reappearance (Bennett and Barnes, 2003, 2004; Orban de Xivry et al., 2006). This predictive reacceleration of the eye is called predictive recovery. Moreover, the observed decrease in eye velocity during blanking is compensated by saccades such that the total amplitude of saccades is inversely proportional to the pursuit displacement (Orban de Xivry et al., 2006, 2008; Coppe et al., 2012). Indeed, saccades compensate for the variability of the smooth eye displacement during

91 blanking and contribute to the predictive mechanisms that improve the perception of
92 the target at reappearance. This synergy between pursuit and saccades is regulated
93 on a trial-by-trial basis by internal models of the eye and target motion.

94 In the present study, we will use these behavioral markers of predictive abilities and
95 internal models in order to characterize the developmental time course of these
96 mechanisms during childhood.

Materials and Methods

Subjects

Eye movements were recorded in a total of 60 subjects categorized in 6 groups of 10 subjects ranging from 5 years to adults (5 groups of children: 5-7,8-10,11-13,14-16,17-19 years and one group of adults: 20-34 years). All subjects were healthy and had normal or corrected to normal vision. All procedures were approved by the Université catholique de Louvain Ethics Committee and were in accordance with the Declaration of Helsinki. Written consents were obtained from the participants or from their parents if they were under 18 years old.

Experimental set-up

The stimulus was projected on a screen (195x145 cm) placed 1.5m away from the subjects with a cine8 Barco projector (refresh rate: 100 Hz; Barco). Eye movements of the dominant eye were recorded with the Eyelink 1000 (SR Research, Ottawa, Canada) at 1000Hz. The dominant eye was determined using a classic test where subjects have to look at a focus point through a small hole made in a sheet of paper. Using the hole as viewing window, only one eye may fixate the focus point. Covering one eye or the other, we determine the dominant fixating eye. Chin and forehead supports were used to stabilize the head.

Paradigm

Subjects were asked to pursue a red dot (diameter of 0.6 deg) centered in a small green bird (width of 4 deg) moving horizontally on the screen (Fig.1). Each trial started with an initial fixation of 1s on one side of the screen at a position randomly

selected between 16 and 25 deg to the left or to the right of the screen center (the head of the bird was oriented in the direction of its future motion). Then, the visual stimulus disappeared for 300ms (gap period) before starting to move at a constant velocity of 15 or 20 deg/s towards the center of the screen. In control trials, the target stayed visible throughout the trial and moved at constant velocity (15 or 20 deg/s) for 2s. In the test trials, after 0.6s of visible motion, the target was blanked for 0.8s (blanking period) and then reappeared and continued to move for another 0.6s (Fig. 1). Subjects were instructed to follow the target as accurately as possible even when the target was not visible. In 10 randomly chosen test trials of each block, the bird that was green before the blanking period reappeared blue after it. In this case, the subjects were instructed to press any key of the keyboard placed in front of them to report this change of color. This color change detection task was used to maintain attention. Each subject performed 8 blocks of 20 trials. Each block consisted of four control trials (trials 1; 2; 9 or 10; 13, 14 or 15) only used to reinforce the continuous movement of the target and 16 test trials. Target direction and velocity were kept constant within a block but randomized across blocks.

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Data analysis

Data analysis was similar to the one described in (Coppe et al., 2012). Eye movements were low-pass filtered at 50 Hz with a bidirectional autoregressive zero-phase filter implemented in MATLAB (de Brouwer et al. 2001). Velocity and acceleration signals were obtained from position with a central difference algorithm on a 20 ms window. Saccades onset and offset were detected based on an acceleration criterion of 500°/s^2 and a minimum duration of 30ms. These saccades

were removed from the velocity traces to analyze the smooth pursuit performance. Saccades were replaced by a linear interpolation between the velocity before and after each saccade.

Each block was divided in 4 periods of 5 trials. Control trials were removed for the analysis. Each period therefore contained between 3 and 5 test trials (T1: trials 3-5 (Early trials), T2: trials 6-10, T3: trials 11-15, T4: trials 16-20 (Late trials)). All trials with blinks during the blanking period were removed from the analysis (3%).

We analyzed separately the anticipatory pursuit response (during the gap period) and the predictive pursuit response (during the blanking period).

In all trials, we quantified the anticipatory pursuit with the gain at trial onset. This gain was computed as the ratio between eye velocity at the onset of target motion and the target velocity.

In test trials, we computed the visually guided gain, the residual gain and the predictive reacceleration during the blanking period to quantify the predictive smooth pursuit. The visually guided gain was defined as the mean eye velocity in a 50ms interval centered 100 ms before target blanking divided by target velocity (illustrated Fig. 4B). When the target disappeared, the eye velocity exponentially decayed to a plateau level called residual velocity (Becker and Fuchs, 1985). The residual gain was defined as the ratio between the mean residual eye velocity in a 50 ms interval centered 500 ms after blanking onset and target velocity (Fig. 4B). This time interval was chosen to fall before any predictive increase in eye velocity observed in the last trials of the block. Predictive reacceleration was defined as the slope of the regression line fitted on the desaccaded eye velocity between 100ms before and 50 ms after the end of target blanking (Fig. 4B).

Saccades were defined as predictive when executed between 120ms and 800ms after target blanking onset. This interval was used as we observed a clear transition in the saccade latency histogram between visually-guided saccades and predictive saccades. A similar transition was observed in an earlier study (Orban de Xivry et al., 2009). Therefore, this interval excludes visually guided saccades from these analyses.

To analyze the saccades executed during the blanking period, we built heat maps of saccade end points for each age group. For heat maps of saccade end points, each ending point (in position and time) was replaced by a 2D Gaussian. The x-coordinate of the center of the 2D Gaussian was the time from target blanking onset when the saccade ended and the y-coordinate of the center of the Gaussian was the horizontal position of the saccade end point. The height of each Gaussian for one participant was equal to 1/n, where n is equal to the total number of saccades elicited by all participants of this age group during the blanking periods. The standard deviation of the Gaussian was 25ms along the x-axis and 0.25deg along the y-axis. Data from all subjects belonging to a given age group were pooled together to build the heat map of this age group.

Position error (PE) at the end of blanking is an additional indicator of how subjects predict target blanking. PE at the end of blanking was defined as the difference between target and eye position at the end of target blanking.

Finally, as saccades and pursuit alone can be predictive, the combination of both types of eye movements can also be a marker of prediction. To study saccade-pursuit interaction, we first computed the distance travelled by saccades during blanking (sum of the saccadic amplitudes during the blanking period) and normalized

this distance by the target displacement (target velocity x blanking duration) in order to obtain the saccadic eye displacement (SAD). The smooth eye displacement (SED) was defined as follows:

$$SED = \frac{Total\ eye\ displ. - Sum\ of\ saccade\ amplitudes}{Target\ displ.}$$

In other words, the saccadic eye displacement was removed from the total eye displacement during the blanking period and normalized to the target displacement to obtain the smooth eye displacement (SED). For each subject separately, a regression line was fitted in order to quantify the relationship between SAD and SED. For this particular analysis, trials with no saccades were excluded. We used the slope of the regression as well as the root mean square error (RMSE) of the fit to quantify the quality of the relationship. Since SAD and SED are proportions, none of these parameters (SAD, SED, slope or RMSE) have units.

Due to the presence of noise in the measure of SED, we performed a control analysis by using the maximum likelihood approach described in Haith et al., 2015. For each measure, the likelihood is given by:

$$L_i \sim \int exp\left[-\frac{(e - SED_i)^2}{2\sigma_{SED}^2} - \frac{(SAD_i - (a\ e + b))^2}{2\sigma_{SAD}^2}\right] de$$

In this expression, e represents the possible values for SED given the noisy measure SEDi. The values of σ_{SAD} and σ_{SED} which represent the variability associated with the SAD and SED measures, were set to 0.2 and 0.1 respectively. A trapezoid integration over e was used to compute the likelihood. The sum of the likelihood over all observations of a subject was computed and we found the values of a (slope of the regression) and b (intercept of the regression) that maximized this log-likelihood.

For all analyses, data from both target directions were collapsed because none of the studied parameters was influenced by the direction of the target motion. Furthermore, the results from both target velocities were averaged since all the results were the same for both target velocities. The use of two target velocities only increased the randomization and task difficulty. For the different parameters, we performed repeated measures ANOVA with age group as between-subject factor and period (T1, T2, T3, T4) as within-subject factor. Main statistical analyses were performed using R. Regression parameters were computed using the robustfit function in MATLAB

Finally, to control the attention of subjects, we used the detection task that involved responding to a color change of the target that may have occurred during the blanking. The percentage of correct color change detection was used as a first way to assess the absence of difference in attention/fatigue between subjects.

In addition, we used the pursuit gain on the control trials (target continuously visible) as a second marker of attention. This gain was computed on a 50 ms interval centered 500 ms after that the target started to move. Three different periods were defined for this analysis: the 2 first control trials, the third control trial and the last one.

Results

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In this experiment, we investigated the ability of children to track a moving target that is transiently blanked and how this ability evolves with age. Typical oculomotor responses from one of the youngest children and one adult are displayed in Fig. 2 and will be used to describe qualitatively the main results of this study. Quantitative analyses will then be reported in details. Both subjects tracked the moving target accurately when it was visible. When the target was blanked (start of the second gray area), the eye velocity of both children and adults rapidly dropped as reported in earlier studies (Fig. 2C and 2D). During the first trials of each block, the eye velocity continued to decay until target reappearance and increased again when the visual feedback became available again (e.g. Fig. 2C). In adults, after a few trials, subjects anticipated the time of target reappearance and the eye reaccelerated before target reappearance (Fig. 2D). During the blanking periods, both smooth pursuit and saccades were combined to pursue the invisible target (Fig. 2B). However, adults had a higher tendency to execute saccades than children (Fig. 2B compared to Fig 2A). A better synergy between saccades and pursuit during blanking in adults led to differences in the position error at target reappearance (Fig. 2B compared to Fig 2A).

This difference in the error at target reappearance was confirmed at the group level. While the younger children lag the target at its reappearance, adults tend to lead it (Fig. 3: main effect of age group on position error: $F(5,54)=5.611$, $p<0.001$). It is worth noting that leading the target at its reappearance is intuitively more appropriate since eye velocity is lower than target velocity. In the following sections, we analyzed specifically three aspects of the oculomotor response during the blanking period. We

first analyzed the pursuit component of the response during the blanking period, we then quantified the saccadic component of the response and finally we analyzed the saccade pursuit interaction. We performed these analyses in order to identify which component of the oculomotor response had the largest impact on the position error at target reappearance.

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Similar pursuit behavior during blanking across age

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Overall, the smooth pursuit behavior was very similar across age groups for the range of target velocity tested. All subjects had similar visually-guided pursuit (no main effect of age group on visually guided pursuit gain: $F(5,54)=1.15$, $p=0.34$, Fig. 4A and B). Hundred milliseconds after target blanking onset, the eye velocity started decreasing exponentially until a plateau (fig. 4A and 4B). The decrease in eye velocity was observed for all age groups and on average the velocity reached the same plateau level for all age groups. The residual gain computed 500ms after target disappearance did not depend on age (Fig. 4C, no main effect of age group: $F(5,54)=0.51$, $p=0.77$) but slightly increased with training for all age groups (main

effect of period: $F(3,162)=10.41$, $p<0.001$ but no interaction between periods and age groups: $F(15,162)=1.35$, $p=0.17$).

For all age groups, the eye velocity initially decayed until around 100ms after target reappearance when the visual feedback became available (Fig. 4A). However, after the three first test trials adults and adolescents learned to increase their eye velocity before the end of the blanking period (light and dark blue traces Fig. 4A and 4B). This predictive recovery of eye velocity was absent in the youngest children (green trace of Fig. 4B). To quantify the predictive recovery, we measured the acceleration of the eye at the end of the blanking period. This predictive recovery was negative for all age groups for the first three trials (T1) and increased after (T2, T3, T4) (main effect of period: $F(3,162)=8,74$, $p=2.10^{-5}$). However, this increase was similar across age groups (interaction between periods and age groups: $F(15,162)=1.28$, $p=0.22$).

In addition, the anticipatory pursuit observed in the gap period was similar across age (no main effect of age on the gain at trial onset: $F(5,54)=0.48$, $p=0.78$ and no interaction between periods and age groups : $F(15,162)=1.05$, $p=0.40$).

Overall, this suggests that predictive smooth pursuit did not differ largely across age groups and might not be responsible for the rather large difference observed in position error at target reappearance.

Saccades land ahead of the target for all age groups.

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In most trials (69 %), at least one saccade was executed during the blanking period in order to compensate for the decrease in eye velocity. However, this percentage largely varied with age (Fig.5). The number of saccades was much lower in the youngest children (Fig. 5A) than in adults (Fig. 5F) and gradually increased with age (Fig. 5G, main effect of age on the number of predictive saccades $F(5,54)=5.71$, $p<0.001$).

In addition, heat maps of saccade endpoints (insets in Fig 5A to F) revealed that saccades of all age groups mainly landed ahead of the position of the invisible target (white line). However, the variability in saccades endpoints appears larger for the younger children (Fig. 5A). These two observations were quantified by the mean and standard deviation of the position error at the end of saccades. The mean position error appeared similar across age groups (Fig 5H, Kurskal-Wallis test: $\chi^2(5,N=54)=2.66$, $p=0.75$) whereas its standard deviation was not (Fig 5I, $F(5,54)=4.22$, $p=0.003$). It was larger for the youngest children than for all the other age groups (Tukey HSD $p<0.03$ for all age groups except children aged 17-19y, $p=0.065$). Therefore, the endpoint of saccades does not seem to be responsible for the observed position error at reappearance since the position error at the end of saccades does not change with age.

The ability to compensate for one's own variability improves with age

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On a trial-by-trial basis, the amplitude of saccades during blanking needs to be adjusted to the decrease in eye velocity in order to align the eye with the target at its reappearance. That is, during the blanking period, the amplitude of the predictive saccades should be larger when the eye velocity drops more and vice-versa (see Fig. 6A and B). Because there is no visual information on the screen, the subjects need to rely on an internal model of their eye movements in order to estimate the decrease in eye velocity and to adjust their saccade amplitude on the flight. For each subject, we quantified the relationship between the amount of distance covered by saccades (saccadic eye displacement (SAD)) as a function of the smooth eye displacement (SED, which is the integral of the smooth eye velocity during the blanking period). The smooth eye displacement can be quite variable on a trial-by-trial basis (see variability of the value on the x-axis Fig. 6A and B). As reported before (Orban de Xivry et al., 2006, 2008; Coppe et al., 2012), adults were able to adjust the amplitude of their predictive saccades to the actual drop in eye velocity on a trial-by-trial basis (Fig. 6B). Such good compensation gave rise to a strong relationship between SAD and SED. This relationship was quantified by the slope of the regression line (Fig. 6B: slope = -1.2) and by the root mean square error (RMSE) around the regression line (Fig. 6B: RMSE=0.19). Perfect compensation would give rise to a slope of -1 and a RMSE of zero. In contrast, young children did not compensate for their eye velocity variability as well as adults (Fig. 6A: slope = -0.5, RMSE = 0.33). This worse compensation gave rise to a lower slope in absolute value and a larger RMSE.

Given that there is no visual information during the blanking period, this compensation can only take place thanks to an internal estimate of eye displacement. The developmental evolution of internal models can thus be assessed

by quantifying the evolution of the strength of the relationship between SAD and SED across age. The absolute value of the slope showing the relationship between SAD and SED increases with age (Fig. 6C; significance of slope: $t(48)= -3.91$, $p<0.001$) and became on average close to -1 in adulthood (Fig. 6C). Similar results are obtained if the slopes are computed using a maximum likelihood approach (see methods) where the noise in the measurement of SED is specifically taken into account (correlation between the slopes and age, $r=-0.48$, $t(48)= -3.78$, $p<0.001$). In addition, the quality of the linear fits (how dots are scattered around the line) also improves with age (Fig. 6D). Indeed the RMSE of the regression decreases with age (significance of the slope: $t(48)= -3.64$, $p<0.001$).

Interestingly, the quality of saccade-pursuit interaction (slope in Fig. 6C) is strongly correlated with the position error at target reappearance ($r(58)=0.7$, $p<0.001$, Fig. 3) as shown in Figure 6E. Furthermore, this relationship stays significant if the effect of age is taken into account (partial correlation $r(56)=0.63$, $p<0.001$). In particular, an ideal slope of -1 yields on average a zero position error of the eye at target reapperance (the regression line in Fig. 6E crosses the (-1,0) point).

Finally, it is worth mentioning that there is also a strong correlation between the variability of the saccade-pursuit interaction (RMSE in Fig. 6D) and the variability of the position error at target reappearance ($r(58)=0.83$, $p<0.001$, Fig. 6F). Thus it can be hypothesized that both average position error at target reappearance and the variability of this parameter are explained by the quality of the saccade-pursuit interaction (slope and RMSE) for each subject, i.e. by the quality of their internal model.

Similar attention with age

Our results cannot be explained by a change in attention as we did not detect such a change. Indeed, age did not influence any of our two markers of attention. First, the percentage of correct color change detection did not change with age (Main effect of the age group: $F(5,54)=0.71$, $p=0.61$). The mean percentage was 92.9 % and ranged from 85.8% for children aged 5-7 years to 99.8% for children aged 8-10 years (and to 89.3% for adults). Second, a differential decrease in pursuit gain on control trials could reflect a difference in attention/fatigue with age. This gain decreased across the time course of a block (Main effect of Period: $F(2,108)=24,9$, $p<0.001$) but did not change differently with age (No main effect of Age group $F(5,54)=1.04$, $p=0.4$ and no interaction Age group x Period: $F(10,108)=1.36$, $p=0.21$).

Discussion

In the present paper, we studied the development of predictive visual tracking and internal models during childhood. Overall, all children starting at 5 years old exhibited some predictive tracking during the blanking period and their oculomotor behavior was similar to the adults. Beside this similarity, we found that the youngest children (aged 5-7y) lack from anticipation in predictive pursuit. In addition, the number of predictive saccades gradually increased with age and the landing position of these saccades was more variable in the youngest children. Finally, our results allow us to precisely identify the development of internal models in children, as measured by the ability of the children to adjust their saccade amplitude to the variability of their smooth pursuit response on a trial-by-trial basis.

The oculomotor behavior of children is close to adult starting at 5 years old

Overall, 5 year old children presented a general oculomotor behavior during blanking that was close to the one previously observed in adults (Becker and Fuchs, 1985; Bennett and Barnes, 2003, 2004, 2005, 2006; Orban de Xivry et al., 2006, 2008; Bennett et al., 2007; Coppe et al., 2012). First, the predictive smooth pursuit response during the blanking period was globally similar across age groups. For instance, at the time of target disappearance, the eye velocity started decreasing to a plateau level that was not significantly different with age. However, adults but not the youngest children were able to reaccelerate their eyes slightly before target reappearance. This predictive recovery relies on the integrity of the frontal lobe (among others), which plays an important role in the spatial representation of an invisible moving target (Barborica and Ferrera, 2003, 2004; Xiao et al., 2007; Ferrera and Barborica, 2010). Predictive recovery is specifically altered in patients with

frontotemporal lobar degeneration (Coppe et al., 2012). The maturation of the frontal zone of the brain during childhood comes late in adolescence (after 16 years) (Giedd et al., 1999; Sowell et al., 1999; Gogtay et al., 2004; Paus, 2005). However, we found only slight improvement with age in the predictive recovery. Despite a tendency for adults to have a higher predictive recovery than other age groups, no statistical differences could be found in this measure that is particularly sensitive to noise. Only the youngest children did not show such a predictive recovery. The absence of predictive recovery could be a sign of a late development of the representation of target displacement.

Second, both children and adults used a combination of smooth pursuit and saccades during blanking, even though the number of saccades triggered during the blanking period increased dramatically with age (see Fig. 5G). From age 5, children executed saccades that landed ahead of the invisible target. Again, this position lead of the eye with respect to the target was comparable across age groups although the variability of this measure decreased with age.

Finally, the timing of the saccades during the blanking period was qualitatively similar across ages. For instance, we observed in all age groups a large drop in the number of saccades around 120ms after disappearance as previously documented (Orban de Xivry et al., 2009).

A lower sensitivity to error may explain the increased error at reappearance in the youngest children

We used the position error at reappearance as a marker of the visual tracking performance of the blanked target. The increased position error of the younger children is the consequence of the low-quality saccade-pursuit interaction as well as

the higher number of trials without predictive saccades during blanking. This number of saccades gradually increases with age. This reveals that older children and adults tend to correct more their movement in absence of visual feedback. The “accuracy” of saccades endpoint during blanking suggests that even the youngest children have some estimate of the target displacement. However, the fact that in youngest children the variability of the saccadic response is much larger (Fig. 5I) and that they trigger much less saccades during blanking (Fig. 5G) is fully compatible with the hypothesis that their internal models are less mature than those of older subjects.

The rate of catch-up saccades was previously found to increase with age during visually guided pursuit (Ego et al., 2013). This increase was associated with an increased sensitivity to errors, a progressive maturation of internal models and a decrease of processing delays. A study on drawing movements (Contreras-Vidal, 2006) also reported a greater endpoint variability for the youngest children (between 5 and 7 years). They attributed this phenomenon to a better internal representation of target position with increasing age.

Precision of internal models improves with age

We found that the variability in the smooth pursuit response during blanking is better compensated by the saccadic system with increasing age. This improved coordination between smooth pursuit and saccades, which also partially determined the average position error at the end of the blanking, relies on the ability to correctly monitor the target, but also the eye position. Since there is no visual feedback during blanking and since proprioception is not available online to the oculomotor system (Wang et al., 2007), this eye position estimation (or eye state) relies on the integrity/maturity of a representation of the eye position by an internal model (Miall

453 and Wolpert, 1996; Wolpert et al., 1998; Shadmehr et al., 2010). A correct internal
454 model of the target displacement is also essential for the interaction between
455 saccade and pursuit. However, the interaction is independent of the reliability of
456 timing estimation since adults present this interaction even when the duration of the
457 blanking period is not predictable (Orban de Xivry et al., 2008).

458 Our results show that children have a good estimate of the target displacement
459 during blanking. Indeed, heat maps show that, even for our youngest children, the
460 saccades landed ahead of the target. This suggests that children have an internal
461 model of the target displacement, which might reside either in the frontal eye field
462 (FEF: Barborica and Ferrera, 2003; Xiao et al., 2007) or in the cerebellum
463 (Cerminara et al., 2009). However, the increased variability of saccade landing
464 positions during blanking together with the reduced synergy between saccades and
465 smooth pursuit in the youngest children indicates that these internal models might
466 still be immature. This late immaturity is consistent with our previous work (Ego et al.,
467 2013) where we found that reflexive oculomotor responses to visible targets followed
468 a similar developmental time course to the time course of predictive internal model
469 maturity reported in this study (evolving throughout adolescence).

470 In young children, the increased uncertainty about the estimated eye position with
471 respect to the target during the blanking period refrains them from executing
472 predictive saccades as they cannot accurately localize the target position with
473 respect to their eye. This unreliability of the internal models of young children
474 contrasts with their rate of saccadic adaptation. Indeed, young children adapt at the
475 same speed as adults (Salman et al., 2006a; Doré-Mazars et al., 2011). The scarcity
476 of predictive saccades observed in the present study and the use of compensatory
477 strategies for lifting or tracking objects reported for young children in another study

(Gachoud et al., 1983) suggests that the central nervous system of young children is well aware of the unreliability of its internal models.

Finally, an interesting comparison can be made between the maturation of children in motor adaptation tasks and in our oculomotor task. Indeed, it has been reported that motor adaptation in a simple reaching task is mature as early as at 6 years old (Takahashi et al., 2003). This contrasts with the report made by Vasudevan et al. (2011) on the development of locomotor adaptation in a split-belt paradigm where it was shown that some aspects of adaptation (timing) are mature as early as 3 years while others (spatial) show slower adaptation rates until 12 years. This is compatible with our results showing a dramatic effect of age on spatial accuracy (position error) in comparison with its effect on timing (predictive recovery). Vasudevan et al. (2011) made the interesting hypothesis that these differences might be due to the complexity of the task, the split-belt paradigm involving the adaptation of a much more complex system with multiple joints. The link could be made with the maturation of the different parts of the cerebellum as revealed by magnetic resonance, with the midline cerebellum (involving the vermis) being mature much earlier than the hemispheres (Hashimoto et al., 1995; Ten Donkelaar et al., 2003; Tiemeier et al., 2010). Thus one could speculate that simpler aspects of motor control (single joint motor adaptation or saccades) might be mature earlier because they rely more on the vermis. In contrast, more complex mechanisms (multiple joint motor adaptation or saccade-pursuit interaction) might become mature later because they rely more on the intermediate and lateral parts of the cerebellum. This possible interpretation is consistent with earlier studies showing that the lateral cerebellum is involved in the implementation of forward models (Pasalar et al., 2006; Miall et al., 2007), which are critical to control the interaction between saccades and pursuit.

Funding

This work was supported by the Belgian Program on Interuniversity Attraction Poles initiated by the Belgian Federal Science Policy Office, Actions de Recherche Concertées (French community, Belgium) and the European Space Agency (ESA) of the European Union. JJO was supported by the Brains Back to Brussels program from the Brussels Region (Belgium). CE was supported by Fondation JED Belgique.

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652 proprioceptive signal in area 3a of somatosensory cortex. *J Neurophysiol* 106: 71–7,
653 2011.

654

Legends

Fig 1. Time course of a (test) trial. After 1s of fixation and a gap period (target blanked for 300ms), the target started moving horizontally at a constant velocity. After 600ms, the target was blanked for 800ms (blanking period) and continued moving for another 600ms. Target velocity (15 or 20 deg/s) and direction (to the left or to the right) were randomized across blocks but kept constant within a block. Each frame in the figure corresponds to a specific period of the trial, with duration reported in parentheses.

Fig 2. Typical trials. A-B: Position of the eye during typical test trials from a young child and an adult and C-D: the corresponding desaccaded eye velocities. Bold parts represent saccades on the position graphs and the timing of saccades on desaccaded eye velocity graphs. Dashed lines represent respectively the target displacement or velocity.

Fig 3. Position error between the eye and the target when the target reappears at the end of the blanking period. Younger children tend to lag the target at reappearance (positive error) whereas older children and adults tend to slightly lead the target when it reappears. Data points are the average values per age group computed with the means by subjects. Error bars are standard errors of the means.

Fig 4. Predictive smooth pursuit. A: Mean eye velocity per age group for the 3 first test trials of each block. B: Mean eye velocity per age group for the 5 last test trials of each block. Grey areas represent the gap and blanking periods (when the target is not visible on the screen). C: Evolution of the residual gain through the blocks for the different age groups. D: Evolution of the predictive

679 recovery through the blocks for the different age groups. For these two last
680 panels, data points are the average per age group computed with the means
681 by subjects. The error bars represent the standard error of these means.
682 Residual gains and predictive recovery are averaged across the two target
683 velocities.

684 Fig 5. Development of predictive saccades with age. A-F: Histograms of the number
685 of saccades during blanking per age group. The time zero corresponds to the
686 onset of target blanking. On the top of each panel there is a heat map of
687 predictive saccades endpoints that shows where the saccades land in space
688 and time. The red color represents the locations in space and time where the
689 eye lands with a high frequency and the blue color locations with nearly no
690 saccade endpoints. The white line represents the virtual target displacement
691 when blanked. G: Evolution with age of the number of predictive saccades
692 during blanking. H: Evolution with age of the mean position error (PE) at the
693 end of each predictive saccade. I: Evolution with age of the standard deviation
694 of PE that represents the variability in space of the saccade endpoints. For
695 these three last panels, data points are the average per age group computed
696 with the means by subjects. Error bars represent the standard error of the
697 means.

698 Fig 6. The interaction between smooth pursuit and saccades improves with age. A
699 and B: Two typical examples of the relationship between the saccadic eye
700 displacement (SAD) and smooth eye displacement (SED) for a young child (6
701 years) and an adult respectively. The colored lines represent the regression
702 line fitted on all the disks (SAD different from zero). The dashed lines are the
703 optimal slopes. C: Evolution with age of the slope of the regression line. Each

dot is the slope for each individual subject. D: Evolution of the quality of the relationship between SAD and SED with age. Each dot represents the root mean square error (RMSE) from the regression for each individual subject. E: Relationship between the position error at target reappearance and the quality of the saccade-pursuit interaction (slope in panel C), F: Relationship between variability of the position error at target reappearance (SD) and the variability of the saccade-pursuit interaction (RMSE in panel D). In Panel E and F, each dot represents an individual subject.

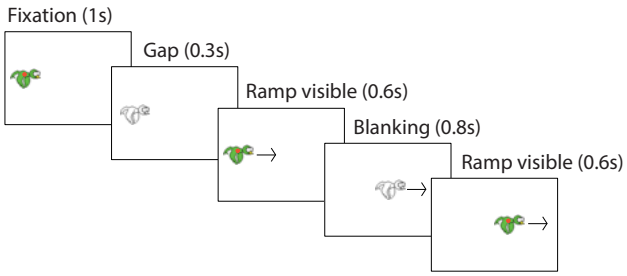
Fixation (1s)
Gap (0.3s)
Ramp visible (0.6s)
Blanking (0.8s)
Ramp visible (0.6s)

Figure 1

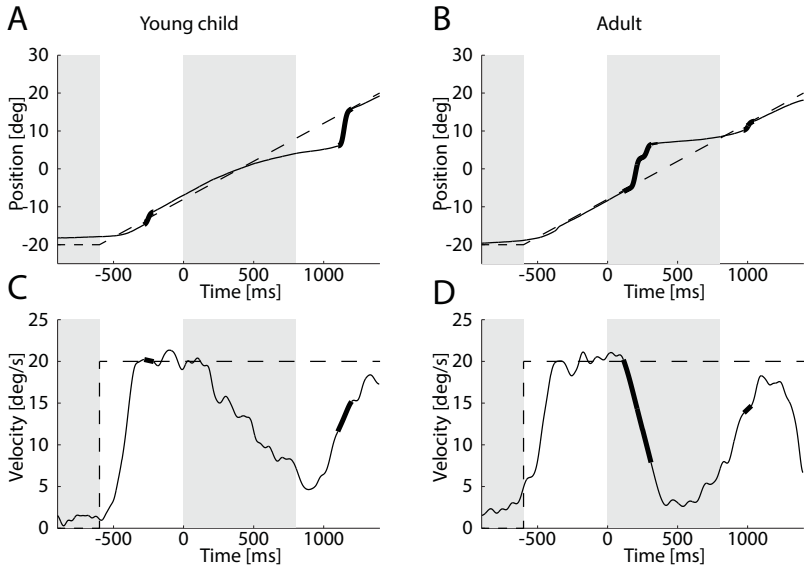
A
Young child
B
Adult
Position [deg]
30
20
10
0
-10
-20
-500
0
500
1000
Time [ms]
C
D
Velocity [deg/s]
25
20
15
10
5
0

Figure 2

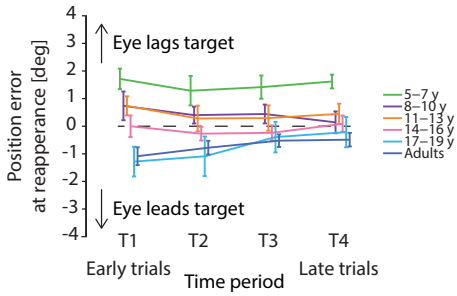
Position error
at reapperance [deg]
4
3
2
1
0
-1
-2
-3
-4
Eye lags target
Eye leads target
T1
T2
T3
T4
Early trials
Late trials
Time period
5–7 y
8–10 y
11–13 y
14–16 y
17–19 y
Adults

Figure 3

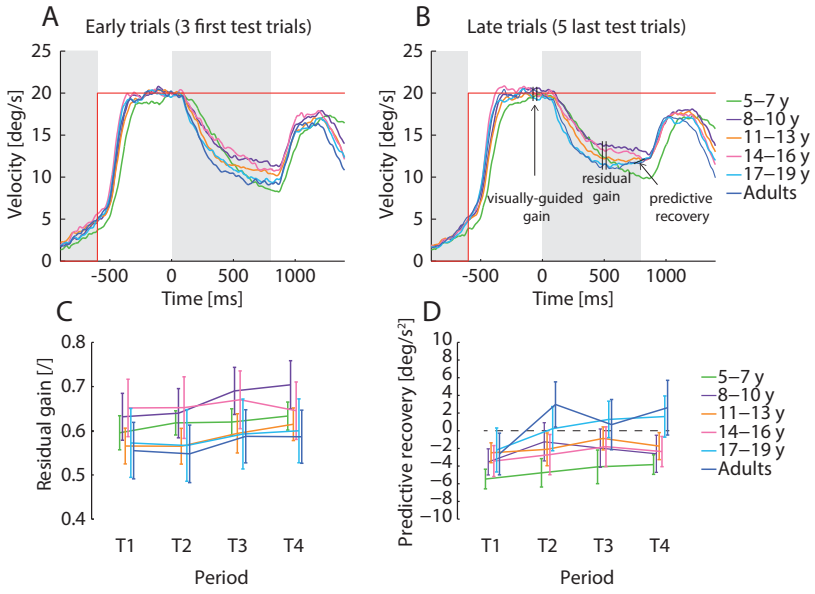
A
Early trials (3 first test trials)
B
Late trials (5 last test trials)
Velocity [deg/s]
Time [ms]
visually-guided gain
residual gain
predictive recovery
5–7 y
8–10 y
11–13 y
14–16 y
17–19 y
Adults
C
Residual gain [/]
D
Predictive recovery [deg/s²]
T1
T2
T3
T4
Period

Figure 4

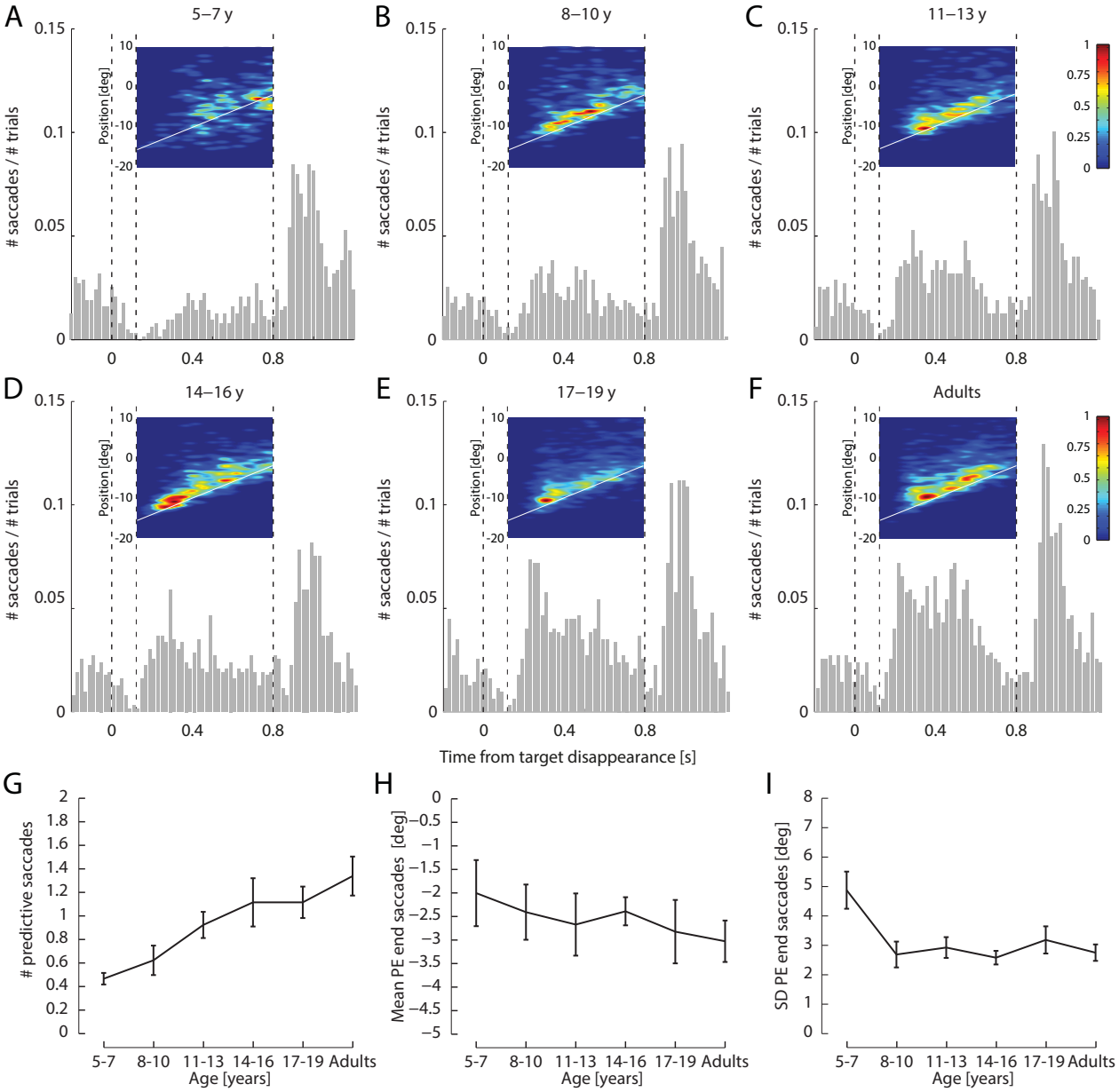
A
5–7 y
B
8–10 y
C
11–13 y
D
14–16 y
E
17–19 y
F
Adults
saccades / # trials
Position [deg]
Time from target disappearance [s]
G
predictive saccades
H
Mean PE end saccades [deg]
I
SD PE end saccades [deg]
5-7
8-10
11-13
14-16
17-19
Adults
Age [years]

Figure 5

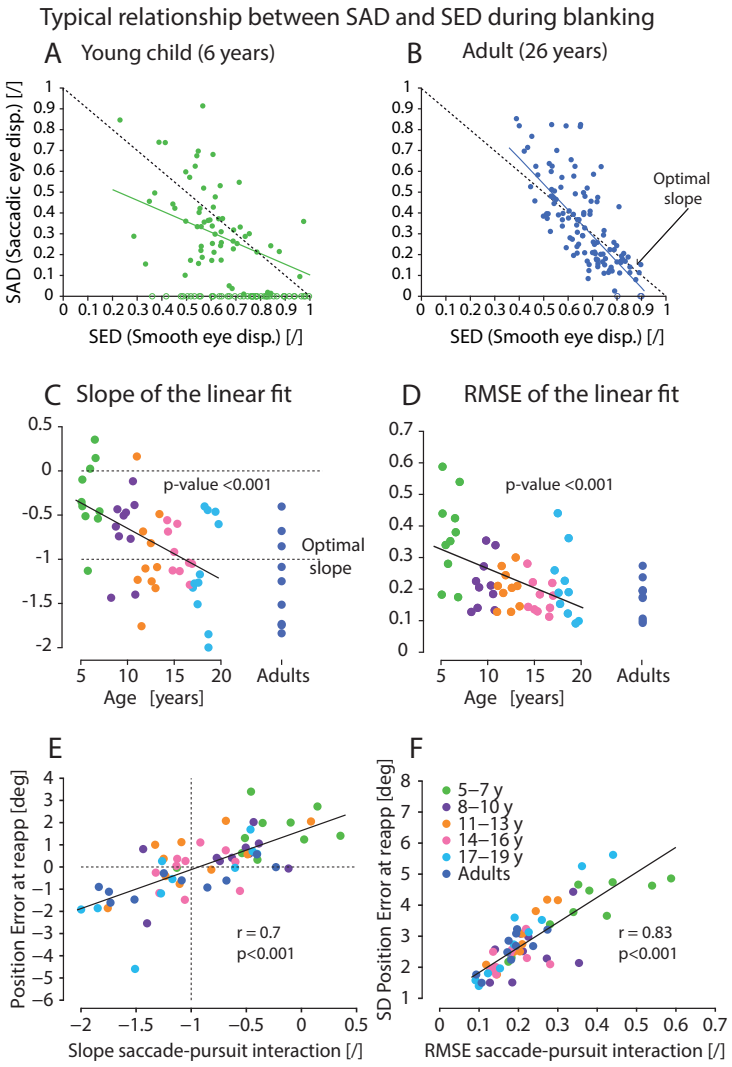
Typical relationship between SAD and SED during blanking
A Young child (6 years)
B Adult (26 years)
SAD (Saccadic eye disp.) [/]
SED (Smooth eye disp.) [/]
Optimal slope
C Slope of the linear fit
D RMSE of the linear fit
p-value <0.001
Optimal slope
Age [years]
Adults
E
F
Position Error at reapp [deg]
SD Position Error at reapp [deg]
5–7 y
8–10 y
11–13 y
14–16 y
17–19 y
Adults
r = 0.7
p<0.001
r = 0.83
p<0.001
Slope saccade-pursuit interaction [/]
RMSE saccade-pursuit interaction [/]

Figure 6